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Puga-Gonzalez, Ivan; Hoscheid, Anne; Hemelrijk, Charlotte K.

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ORIGINAL PAPER

Friendship, reciprocation, and interchange in an individual-based model

Ivan Puga-Gonzalez · Anne Hoscheid · Charlotte K. Hemelrijk

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Abstract Reciprocation and interchange of grooming and support may emerge as a consequence of the socio-spatial structure of the group through which individuals interact with certain partners more frequently than with others. This is shown in a computational model of grouping, fighting, and grooming, called Groofiworld. In this case, no specific mechanism of exchange is needed, such as described in calculated reciprocity or emotional bookkeeping. One of the drawbacks of this model, GroofiWorld, however, is that it lacks social bonding, a factor that may play an important role in real societies of primates. To investigate the effect of social bonding on exchange relations, in the present study, we add 'social bonding' to the model 'GrooFiWorld.' In the new model, called 'FriendsWorld,' social bonds or 'friends' are defined as the top 25 % grooming partners and individuals are given a tendency to follow their friends. Note that they do not intend to reciprocate or interchange social services with friends. Results show that this mechanism of 'follow-your-friends,' not only increases social interactions among top grooming partners, but also strengthens the patterns of reciprocation and interchange. Our findings suggest that, in real primates, reciprocation and interchange may emerge as a side-effect of the social–spatial structure of the group and subsequently be strengthened by social bonding as represented in FriendsWorld. We give predictions that distinguish between the mechanism of 'follow-your-friends' and emotional bookkeeping.

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I. Puga-Gonzalez (✉) · A. Hoscheid · C. K. Hemelrijk
Behavioural Ecology and Self-Organization, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands
e-mail: ivanpuga@gmail.com

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Introduction

In primate societies, individuals appear to reciprocate and interchange social services such as grooming, support in fights, food, tolerance, etc. Empirical support for reciprocation and interchange of social services comes mainly from studies which commonly find a statistically significant positive correlation between the number of acts given and received over long periods of time. However, what the mechanisms are regulating reciprocation and interchange of social services at a proximate level is still controversial. Brosnan and de Waal (2002) and de Waal and Brosnan (2006) proposed three plausible different mechanisms with increasing cognitive demands: symmetry-based reciprocity, attitudinal reciprocity, and calculated reciprocity.

Symmetry-based reciprocity is the simplest cognitive mechanism. It assumes that positive correlations between acts given and received may result from a common symmetrical variable within a dyad of individuals. Symmetrical variables include time spent in association, kinship, age, etc. For instance, when individuals direct most of their social acts to those partners with whom they spent most time together, reciprocation, and interchange should automatically emerge (de Waal and Luttrell 1988; Brosnan and de Waal 2002; de Waal and Brosnan 2006). Symmetry-based reciprocity, however, has been disregarded as a plausible mechanism underlying reciprocation and interchange because after partialling out symmetrical variables correlations remain statistically significant (de Waal and Luttrell 1988; Hemelrijk and Ek 1991; Gomes and Boesch 2009).

Calculated reciprocity is the mechanism assuming the most sophisticated cognition. This mechanism requires long-term memory of past events, keeping track of the number of social services given to and received from others, and paying back accordingly (de Waal and Luttrell 1988; Brosnan and de Waal 2002; de Waal and Brosnan 2006). Calculated reciprocity, however, has been criticized because of the difficulty of keeping track of acts given and received over the long-term (Stevens and Hauser 2004), a task that seems difficult even for human primates (Stevens et al. 2011). Therefore, several studies have focused on reciprocation over short periods of time, i.e., short-term contingency. These studies, however, have failed to show evidence for short-term contingency (Schino et al. 2003, 2007, 2009; Manson et al. 2004; Brosnan et al. 2009; Frank and Silk 2009; Jaeggi et al. 2013; Amici et al. 2014; but see Dufour et al. 2009). The lack of evidence for short-term contingency shifted the focus from 'calculated reciprocity' to more parsimonious mechanisms such as 'attitudinal reciprocity' (de Waal 2000) or 'emotional bookkeeping' (Schino and Aureli 2009).

Attitudinal reciprocity was first proposed by de Waal (2000) as a mechanism mediating reciprocity by mirroring the attitudes of social partners in recent social interactions, i.e., '*if you are nice*, *I'll be nice*' (de Waal and Brosnan 2006). This idea was further developed by Schino and Aureli (2009, 2010) to explain reciprocity over the long-term. Schino and Aureli (2009, 2010) proposed emotions as the basis of behavioral decisions and thus, whether an individual reciprocates or interchanges a social act with a partner depends on the type of emotion associated with that specific partner: The frequent receipt of benefits (e.g. grooming, support, food, tolerance, etc.) from a partner over long periods of time elicits the association of a specific emotion with a specific partner which may subsequently motivate it to pay back social services to this specific partner (Schino and Aureli 2009, 2010). Emotions, thus, enable individuals to preferentially interact with those group members that have provided them with most benefits over a long-term period rather than merely based on recent interactions (Schino and Aureli 2009, 2010). This mechanism is called 'emotional bookkeeping.'

Recently, we have proposed an alternative mechanism to explain reciprocation and interchange. This explanation is derived from the model GrooFiWorld, an individual-based model in which individuals tend to remain in a group and interact with those in their proximity by either fighting or grooming with them (Puga-Gonzalez et al. 2009, 2014; Hemelrijk and Puga-Gonzalez 2012). In the model, reciprocation and interchange of grooming and support emerge due to the socio-spatial structure of the group which in turn is a consequence of aggressive interactions among group members. Dominant individuals win most of their fights and chase away subordinates. Consequently, dominants end up in the center of the group whereas subordinates end up at the periphery (Hemelrijk 1999, 2000). This structure determines who encounters whom, causing individuals to interact with some individuals more than with others. Individuals, thus, groom and support certain partners more often than others which causes the emergence of positive correlations between grooming and support given and received (Puga-Gonzalez et al. 2009; Hemelrijk and Puga-Gonzalez 2012). This mechanism is simpler than 'emotional bookkeeping' because reciprocation and interchange emerge as a side effect of the spatial structure and proximity-based interactions without individuals selecting specific partners for reciprocation.

However, the GrooFiWorld model has been criticized for several reasons. First, the mechanism proposed by the model, i.e., spatial structure in combination with proximity-based interactions, is similar to symmetry-based reciprocity, with proximity being the symmetrical variable. Empirical studies, however, discard proximity as a possible factor underlying reciprocation and interchange because, when proximity is partialled out, correlations remain significant (de Waal and Luttrell 1988; Hemelrijk and Ek 1991; Gomes and Boesch 2009). Interestingly, this is also the case in GrooFiWorld. Here too, correlations remain significant after partialling out proximity. Only when proximity is omitted from the interactions, by making individuals interact with random partners, do correlations for reciprocity and interchange disappear (Hemelrijk and Puga-Gonzalez 2012). Second, in GrooFiWorld, individuals have no preference with whom they associate with, whereas several empirical studies show that individuals prefer to associate with some partners rather than others (Tiddi et al. 2011; Sabbatini et al. 2012; Jaeggi et al. 2013). It seems, thus, that 'social bonds' or 'friendships' are important to individuals in real primate societies (Smuts 1985; Silk et al. 2003; Silk 2007; Massen et al. 2010; Berghaenel et al. 2011). Therefore, in the present study, we model a kind of social bonding (i.e., 'friendships') in the form that individuals have a preference to move towards their friends, i.e., they follow them. We call this mechanism 'follow-your-friends.' Our aim is to understand the effects that this mechanism has on patterns of reciprocation and interchange of grooming and support.

The 'follow-your-friends' mechanism was inspired by two empirical facts, first, by the observation that grooming produces a positive emotion (i.e. a state of well-being) in the groomee and groomer (Keverne et al. 1989; Graves et al. 2002; Shutt et al. 2007). From this, we inferred that it does so more strongly the more often individuals have been involved in grooming with another. So, we arbitrarily distinguished between the top quartile being 'friends' and the rest not. Second, it is by the observation of King et al. (2011) that, in baboons, individuals follow their friends. Therefore, in 'FriendsWorld,' individuals prefer to move towards their 'friends.'

Note that the main difference between the mechanism of 'follow-your-friends' and emotional bookkeeping is that, in

the former, individuals lack an intention to reciprocate or interchange services with their 'friends.'

Methods

FriendsWorld is an individual-based, spatially explicit model, written in C++, as an extension of the GrooFiWorld model. The parameter values are the same as in previous versions of the GrooFiWorld model except for group size which was increased from 12 to 16 (Table 1). The model comprises a continuous two-dimensional 'world' (without borders) in which individuals are moving in all directions. Individuals have a fixed vision angle (*VisionAngle*, Table 1) and a maximum perception distance (*MaxView*, Table 1). At the beginning of each simulation, the individuals are located at random locations within a previously defined radius (*InitRadius*, Table 1), calculated by multiplying group size by an arbitrary constant. To regulate the activities of the individuals, each individual is attributed a random waiting time drawn from a uniform distribution, and the individual with the shortest waiting time gets activated first (Hemelrijk 1999; Puga-Gonzalez et al. 2009). These waiting times are combined with a biologically plausible timing regime, reflecting a kind of social facilitation, (Galef 1988) during which an individual's waiting time is reduced when a dominance interaction occurs close by (Radius of social facilitation, Table 1). Intensity of aggression is reflected by the *StepDom* value. Fierce aggression (e.g., bites), as in intolerant primate societies, is represented by high values, and mild aggression (e.g., threats, slaps), as in tolerant societies, is represented by low values (Table 1). To represent sexual dimorphism, males have a higher *StepDom* value than females (Table 1) (Hemelrijk et al. 2008). As in GrooFiWorld, in FriendsWorld, individuals tend to (1) remain in a group, (2) fight, and (3) groom. Why individuals form groups (e.g., for predator avoidance) and fight (e.g., for food or mates) is not specified. Grooming reduces the anxiety of individuals (Keverne et al. 1989; Graves et al. 2002; Shutt et al. 2007).

Friendships

In contrast to GrooFiWorld, in FriendsWorld, individuals categorize others as 'friends' or not. As 'friends' are classified,

Table 1 Default parameter values in friends world

Parameter	Description	Value
General parameters		
Group size	Total number of individuals	16
Sex ratio (at high aggression intensity)	Number of males and females	13 females, 3 males
Sex ratio (at low aggression intensity)	Number of males and females	11 females, 5 males
InitRadius	Predefined radius at start of simulation	(1.7) x (No. Individuals)
Radius of social facilitation	Radius starting from center point of fight	10
Grouping parameters		
PersSpace	Close encounter distance	8
NearView	Medium distance	24
MaxView	Maximal viewing distance	50
SearchAngle	Turning angle to find others	90°
VisionAngle	Angle of field of view	120°
Dominance parameters		
InitDom	Initial Dom value	16 for females, 32 for males
RiskAvers	Number of 'mental battles' before attack	2
StepDom (at high aggression intensity)	Scaling factor for aggression intensity	0.8 for females, 1.0 for males
StepDom (at low aggression intensity)	Scaling factor for aggression intensity	0.08 for females, 0.1 for males
FleeingDist	After losing a fight	2
ChaseDist	Chasing distance after winning a fight	1
Grooming parameters		
InitAnx	Initial anxiety value	0.5
AnxInc	Increase in anxiety after every activation	1 %
AnxDcrGree	Decrease in anxiety in groomee	0.15
AnxDcrGrmr	Decrease in anxiety in groomer	0.1
AnxIncFight	Increase in anxiety after fighting	0.1

those partners with whom an individual was involved in grooming the most, i.e., individuals that were within the top 25 % of ego's affiliation score. The affiliation score is the sum of grooming given and received. It does not involve that individuals keep track of the balance of their grooming relationships.

Grouping rules

In FriendsWorld, individuals are made to follow their 'friends.' Individuals have three different visual ranges: *PersSpace*, *NearView*, and *MaxView* (Table 1). When an individual does not perceive another in its close proximity (i.e., within its *PersSpace*), it acts according to the grouping rules (Fig. 1b). For instance, if an individual perceives one of its top 25 % grooming partners within its *NearView*, it will move one step towards it. If several top 25 % grooming partners are perceived, the individual moves towards the closest one. If none of its top 25 % grooming partners is perceived but other individuals are, the individual just keeps on moving (Fig. 1b). When no others are perceived within *NearView*, the individual looks further away into *MaxView* (Table 1). If other individuals are perceived within *MaxView*, the individual moves towards the closest top 25 % grooming partner if available; otherwise, it moves towards the closest individual (Fig. 1b). If no individual is perceived within *MaxView*, the individual scans for others by turning over a *SearchAngle* (Table 1; Fig. 1b).

Interaction rules

In FriendsWorld, the interacting rules are the same as in GrooFiWorld (Fig. 1a). If the individual perceives another one within its *PersSpace*, a dominance interaction may occur. Whether or not the individual will attack depends on the outcome of a mental battle. If the individual wins the mental battle, it will attack its partner (see "Dominance rules"). However, if the individual loses the mental battle, it will consider grooming instead (see "Grooming rules").

Our previous sensitivity analyses have shown that the results of our model regarding patterns of dominance style, of affiliation, and of coalitions are robust to changes in the order of the interaction rules (Hemelrijk and Puga-Gonzalez 2012).

Dominance rules

Dominance interactions are modelled as in previous models (Hogeweg 1988; Hemelrijk 1999; Puga-Gonzalez et al. 2009) and are extensions of the DoDom rules of Hogeweg (1988). When individual *i* meets individual *j* in its *PersSpace*, individual *i* considers whether it will be able to win a fight against *j* by means of a 'mental battle.' During a mental battle, individual *i* compares its *Dom* value relative to that of *j*; individual *i* expects to win if its relative dominance value is greater than a random number drawn from a uniform distribution between zero and one (Eq. 1). A 'mental battle' may be carried out once or several times, depending on the value of risk aversion (*RiskAvers*, Table 1). The higher the risk

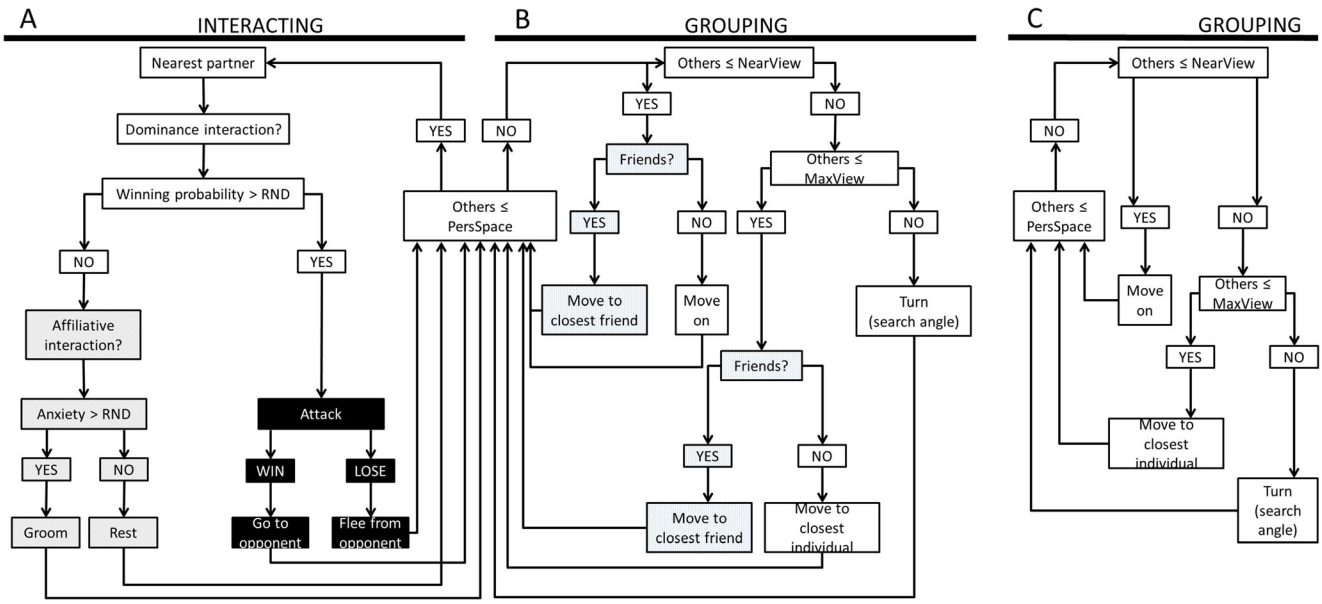

Fig. 1 Rules for interacting and grouping in FriendsWorld and GrooFiWorld. **a** The interaction rules are the same for both models: *Solid black boxes* show the dominance interactions and striped boxes the affiliation interactions. **b** Grouping rules in FriendsWorld, the *white dotted boxes* show the friends rules in *NearView* and *MaxView*. **c** Grouping rules in GrooFiWorld

aversion, the more mental fights an individual must win before it actually attacks its opponent. During an actual dominance interaction, the relative *Dom* value is again compared with a randomly drawn number between zero and one; if the relative *Dom* value is higher than this random number, individual i wins the fight (w_i=1); otherwise, it loses (w_i=0) (Eq. 1):

$$w_i = \begin{cases} 1 & \dfrac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j} > \mathrm{RND}\,(0,\ 1) \\ 0 & \text{else} \end{cases} \qquad (1)$$

To represent self-reinforcing effects of victory and defeat (Hsu and Wolf 1999; Hsu et al. 2006) after a fight, the dominance value of the winner is increased, while that of the loser is decreased by the same amount respectively (Eq. 2),

$$\begin{aligned} \mathrm{DOM}_i &= \mathrm{DOM}_i + \left(w_i - \frac{\mathrm{DOM}_i}{\mathrm{DOM}_i + \mathrm{DOM}_j}\right) * \mathrm{STEPDOM} \\ \mathrm{DOM}_j &= \mathrm{DOM}_j - \left(w_i - \frac{\mathrm{DOM}_j}{\mathrm{DOM}_i + \mathrm{DOM}_j}\right) * \mathrm{STEPDOM} \end{aligned} \qquad (2)$$

Expected outcomes have a lower impact; high-ranking individuals will increase their *Dom* value slightly after winning a fight; however, an unexpected victory from a low-ranking individual will lead to a greater increase in its relative *Dom* value. In order to keep *Dom* values positive, their minimum is set to 0.01. The change in dominance values (*Dom*) is multiplied by a scaling factor between 0 and 1, called *StepDom* (Table 1); a high *StepDom* value indicates fierce aggression, and a low *StepDom* value indicates mild aggression (Hemelrijk 1999). After a fight, the winner chases the loser over a distance of one unit (*ChaseDist*, Table 1), and then it turns randomly 45° to the left or the right. The loser reacts by fleeing over a fixed distance of 2 units (*FleeingDist*; Table 1), and then it turns randomly 45° to the left or right. The turning angle prevents repeated interactions between same partners after a fight.

As in our previous study on coalitions in the GrooFiWorld model (Puga-Gonzalez et al. 2014), in FriendsWorld coalitions emerge as a consequence of 'social facilitation.' When an individual, *C*, close to a fight between combatants *A* and *B*, is activated right after the conflict and attacks one of two combatants (e.g., *B*), this is counted as an act of support (for *A*) and opposition (to *B*)—also called contra-support—as is done when recording behavior of real primates (de Waal and Luttrell 1988; Hemelrijk and Ek 1991; Silk 1992; Widdig et al. 2000, 2006; Silk et al. 2004; Berman et al. 2007; Schino et al. 2007).

Grooming rules

In real primates, grooming is influenced by several physiological conditions, such as stress levels (Sapolsky 1992) and opiate concentrations (Keverne et al. 1989; Graves et al. 2002). These physiological mechanisms are reflected in the model by an anxiety value which ranges from 0 to 1, with 0 being relaxed and 1 being very tense. When an individual decides not to fight, it will consider whether to groom its partner or not, depending on its anxiety value. If its anxiety value is higher than a random number between 0 and 1, the individual will groom its partner; otherwise, it does nothing (Fig. 1a). To prevent repeated interactions between the same partners, after grooming, both partners turn randomly to the left or right over an angle of 45°.

In line with empirical studies, grooming reduces anxiety in both individuals; it does so more in the groomee (*AnxDcrGree*), than in the groomer (*AnxDcrGrmr*) (Table 1); if individuals do not groom for a certain amount of time, their anxiety level increases (*AnxInc*, Table 1) (Keverne et al. 1989; Graves et al. 2002). Since, in empirical studies it has been shown that former opponents increase their anxiety after a fight (Aureli et al. 2002), in the model, anxiety also increases in both opponents after a fight by *AnxIncFight* (Table 1).

Parameters and experimental setup

Parameter values are the same as in previous versions of the GrooFiWorld model except group size which was increased from 12 to 16 individuals (Puga-Gonzalez et al. 2009). This increment in Group size was done in order to increase statistical power and thus point out differences between GrooFiWorld and FriendsWorld. Following empirical studies, sex ratios were biased towards females: At high intensity of aggression (intolerant societies), groups comprised 80 % females and at low intensity (tolerant societies), 70 % (Caldecott 1986; Ménard 2004). To reflect sexual dimorphism, initial dominance values, *InitDom*, were set at 16 for females and 32 for males (Table 1).

Note that, in previous studies, we have shown that the results of the model are robust to changes in the values of the parameters of grooming, dominance, sex ratio, and group size (Puga-Gonzalez et al. 2009; Hemelrijk and Puga-Gonzalez 2012).

Data collection and analysis

Simulations were run at high and low intensities of aggression. Each simulation consists of ten separate runs divided into 260 periods. Each period consists of 320 activations (i.e.,

GroupSize, 16×20). To avoid transient dominance values, data are collected from period 200 to 260 (Hemelrijk 1999; Puga-Gonzalez et al. 2009). Data recorded included the individual's spatial position and its social interactions. During social interactions, we recorded the identities of the winner and loser of a fight and their *Dom* values, as well as the identities of groomer and groomee and their anxiety values. Results are presented as the average of the ten runs, with their combined probability using the improved Bonferroni procedure (Hochberg 1988). To test for differences between high and low intensity of aggression and between GrooFiWorld and FriendsWorld, we use Mann Whitney *U* tests. *P* values are two-tailed.

The percentage of time females spent fighting (or grooming) is measured as the total number of fights (or grooming bouts) in the group divided by total number of activations (Puga-Gonzalez et al. 2009). The steepness of the hierarchy is calculated by obtaining the coefficient of variation of the *Dom* values. For each run, the average value over periods 200–260 is calculated and averaged over the ten runs. The higher the coefficient of variation, the steeper the hierarchy, indicating that differences between ranks are very pronounced (Hemelrijk 1999). Ranks are calculated by averaging the *Dom* values of each individual over periods 200–260. Centrality of individuals is calculated by using circular statistics (Hemelrijk 1999): A circle is drawn around ego, and the direction of the other group members are projected as points on the circumference (Mardia 1972). This measurement returns several vectors. The length of the average vector then represents the amount of clustering found within the group. A long average vector indicates that an individual is found at the periphery of the group. Hence, centrality of dominants is represented by a negative correlation between rank and the length of average vector.

Reconciliation between former opponents is measured via the improved PC-MC method (Post-Conflict versus Matched-Control) (Veenema et al. 1994), which compares the time at which grooming occurs shortly after a conflict, the Post-Conflict period, and the moment grooming occurs in a control period of the same length, the Matched-Control, recorded a day later during the same time. Here, we use the PC-MC method as described in Puga-Gonzalez et al. (2009). Conciliatory tendency is defined in Eq. 3.

$$\text{Conciliatory tendency} = \frac{\text{Number of attracted pairs} - \text{Number of dispersed pairs}}{\text{Total number of conflict pairs}} \quad (3)$$

We used matrix Tau-Kr correlations to test for the distribution of social interactions: grooming, aggression, and reconciliation (Hemelrijk 1990). The level of significance was calculated using 2,000 permutations. Reciprocation of grooming and aggression are tested by correlating an actor and a receiver's matrix. Positive correlations indicate reciprocity and negative correlations indicate uni-directionality (Hemelrijk 1990). Whether grooming is directed up the dominance hierarchy or towards individuals of similar rank is measured by correlating the matrix of grooming given with a partner–rank matrix and a similar–rank matrix respectively. The partner–rank matrix is filled with the average *Dom* values of each partner in the rows. The similar–rank matrix is filled with zeros apart from the partners closest and second closest in rank, which are indicated as 1's. Since higher-ranking individuals have higher *Dom* values, a significantly positive correlation with the partner–rank matrix means that grooming is directed up the dominance hierarchy, while a positive correlation with the similar–rank matrix corresponds to grooming directed towards individuals of similar ranks (Hemelrijk 1990).

The diversity of interaction partners was measured to test whether individuals in FriendsWorld were more selective in their interaction partners than in GrooFiWorld. Two different diversity indices are used: Berger-Parker dominance index (Southwood 1978) and the percentage of non-interacting dyads. In addition, we also measured the stability of the top 25 % of grooming partners during the whole simulation.

The Berger-Parker dominance index is calculated by dividing the frequency of grooming of ego with its favorite partner (i.e., the individual with whom it has the highest number of interactions) by the total grooming frequency of ego with all other individuals (Eq. 4) (Southwood 1978; Hemelrijk and de Kogel 1989). The higher the Berger-Parker dominance index, the less diverse the interacting partners.

$$\text{BP} = \frac{\text{grooming frequency between individuals A \& B}}{\text{Total grooming frequency of individual A}} \quad (4)$$

To calculate the relative number of non-interacting dyads, we count the number of dyads that never interacted and divided it by the total number of possible dyads (i.e., 120).

To analyze the stability of top 25 % of grooming partners, every 20 periods (from period 200 to 260), we recorded, per individual, the percentage of top 25 % grooming partners that remained the same. Results are based on the average percentage of the group per run.

Table 2 Dominance style and affiliative patterns in GrooFiWorld and FriendsWorld

	High intensity of aggression		Low intensity of aggression	
	GrooFiWorld	FriendsWorld	GrooFiWorld	FriendsWorld
Dominance style				
1. Gradient of the hierarchy	0.82	0.88	0.11	0.12
2. Female dominance	0.29	0.31	0	0
3. Unidirectionality of aggression	−0.35**	−0.02**	0.40**	0.48**
4. Centrality of dominants (Tau)	−0.48**	−0.40**	−0.08	−0.20
5 Time spent fighting %	14	18	18	24
6. Average nearest neighbour distance	4.29	3.89	3.6	2.75
Affiliative patterns				
7. Time spent grooming (%)	16	19	20	25
8. Coalitions (%)	9	9	7	8
9. Conciliatory tendency (%)	18	15	30	27
10. Grooming up the hierarchy	0.41***	0.37**	0.11*	0.11*
11. Grooming among similar ranks	0.15*	0.14*	0.07	0.02
12. Reconciliation with valuable partners	0.36**	0.49**	0.04*	0.03

Results are average of ten runs. *P* values are combined via the improved Bonferroni method

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Results

Dominance style and affiliative patterns

As in GrooFiWorld, in FriendsWorld, similar patterns emerge as regards dominance and affiliation and their differences between high and low intensity of aggression (Table 2). In contrast to low intensity of aggression, at high intensity: The gradient of the hierarchy is steeper (1 in Tables 2 and 3, B); females are more dominant over males (2 in Tables 2 and 3, B); aggression is unidirectional rather than bidirectional (3 in Tables 2 and 3, B); centrality of dominants is stronger (4 in

Table 3 Comparison of dominance and affiliative patterns

	GrooFiWorld	FriendsWorld	GrooFiWorld vs FriendsWorld	
	A. High vs. low	B High vs. low	C. High	D. Low
Dominance style				
1. Gradient of the hierarchy	*U*=100***	*U*=100***	*U*=61 NS	*U*=63 NS
2. Female dominance	*U*=95***	*U*=100***	*U*=53 NS	*U*=50 NS
3. Unidirectionality of aggression	*U*=100***	*U*=84**	*U*=72 NS	*U*=74 NS
4. Centrality of dominants (Tau)	*U*=92**	*U*=78*	*U*=57 NS	*U*=53 NS
5. Time spent fighting %	*U*=100***	*U*=100***	*U*=100***	*U*=100***
6. Average nearest neighbor distance	*U*=98***	*U*=100***	*U*=73 NS	*U*=100***
Affiliative patterns				
7. Time spent grooming (%)	*U*=100***	*U*=97***	*U*=76 NS	*U*=100***
8. Coalitions (%)	*U*=96***	*U*=70 NS	*U*=52 NS	*U*=95***
9. Conciliatory tendency	*U*=100***	*U*=100***	*U*=68 NS	*U*=82*
10. Grooming up the hierarchy	*U*=100***	*U*=95***	*U*=57 NS	*U*=52 NS
11. Grooming among similar ranks	*U*=72 NS	*U*=79*	*U*=46 NS	*U*=61 NS
12. Reconciliation with valuable partners	*U*=98***	*U*=100***	*U*=71 NS	*U*=53 NS

Comparison between high and low intensities of aggression in (A) GrooFiWorld and (B) FriendsWorld, and between FriendsWorld and GrooFiWorld at (C) high and (D) low intensities of aggression. Mann–Whitney *U* test

NS not significant

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 4 Reciprocation and interchange of grooming and support in GrooFiWorld and FriendsWorld

	High intensity of aggression		Low intensity of aggression	
	GrooFiWorld	FriendsWorld	GrooFiWorld	FriendsWorld
1. Grooming Reciprocation	0.37***	0.51**	0.45***	0.50***
2. Reciprocity of support	0.35**	0.50**	0.19**	0.23**
3. Support received for grooming given	0.41***	0.55***	0.25**	0.22**
4. Support given for grooming received	0.26**	0.44**	0.30**	0.29**

Tau-Kr matrix correlations, results are average of ten runs. *P* values are combined via the improved Bonferroni method

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Tables 2 and 3, B); time spent fighting is lower (5 in Tables 2 and 3, B); groups are less cohesive (6 in Tables 2 and 3, B); time spent grooming is lower (7 in Tables 2 and 3, B); the percentage of coalitions is higher (8 in Tables 2 and 3, B); reconciliation is less frequent (9 in Tables 2 and 3, B); grooming is directed up the dominance hierarchy and occurs more frequently and among partners of similar rank (10–11 in Tables 2 and 3, B), and individuals reconcile more often with valuable partners (12 in Tables 2 and 3, B).

Comparing FriendsWorld to GrooFiWorld, the patterns of dominance style and affiliation differ mostly at low but not at high intensity of aggression (Table 3, C and D). At high intensity of aggression, only 1 out of 12 patterns differ: In FriendsWorld, individuals spent significantly more time fighting than in GrooFiWorld (5 in Tables 2 and 3, C). At low intensity of aggression 5 out of 12 patterns differ: in FriendsWorld, individuals (1) spend more time fighting (5 in Tables 2 and 3, D), (2) are closer to their neighbours (6 in Tables 2 and 3, D), (3) spent more time grooming (7 in Tables 2 and 3, D), (4) form coalitions more frequently (8 in Tables 2 and 3, D), and (5) reconcile less frequently (9 in Tables 2 and 3, D) than in GrooFiWorld.

Reciprocation and interchange of grooming and support

Patterns of reciprocation and interchange of grooming and support also emerge in the FriendsWorld model, and, except for reciprocation of grooming, all of them are significantly stronger at high than at low intensity of aggression (2–4 in Tables 4 and 5, B). Comparing GrooFiWorld to FriendsWorld, in FriendsWorld at high intensity of aggression, three out of four patterns of reciprocity and interchange are significantly stronger: (1) reciprocity of support, (2) support received for grooming given, and support given for grooming received (2–4 in Tables 4 and 5, C).

Interactions among friends in GrooFiWorld and FriendsWorld

In FriendsWorld at high intensity of aggression, individuals were more selective with their interaction partners: The percentage of non-interacting dyads and the Berger-Parker dominance index were higher than in GrooFiWorld (1–3, in Tables 6 and 7, C). Besides, in FriendsWorld, individuals maintain usually the same top 25 % grooming partners during the whole simulation, whereas in GrooFiWorld individuals change those partners more frequently (4 in Tables 6 and 7, C and D).

In both models, individuals attack and support their top 25 % grooming partners significantly more than other group members (Tables 8 and 9, A and B). Besides, in FriendsWorld at high intensity of aggression, individuals attack and support more their top 25 % grooming partners than in GrooFiWorld;

Table 5 Comparison of Tau-Kr coefficient values of reciprocation and interchange of grooming and support

	GrooFiWorld	FriendsWorld	GrooFiWorld vs FriendsWorld	
	A. High vs. low	B. High vs. Low	C. High	D. Low
1. Grooming reciprocation	U=77*	U=57 NS	U=69 NS	U=69 NS
2. Reciprocity of support	U=85**	U=94***	U=77*	U=71 NS
3. Support received for grooming given	U=92***	U=100***	U=79*	U=64 NS
4. Support given for grooming received	U=66 NS	U=77*	U=76*	U=50 NS

Comparison between high and low intensities of aggression in (A) GrooFiWorld and (B) FriendsWorld, and between FriendsWorld and GrooFiWorld at (C) high and (D) low intensities of aggression. Mann–Whitney *U* test

NS not significant

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 6 Diversity of partners and stability of friends in GrooFiWorld and FriendsWorld

	High intensity of aggression		Low intensity of aggression	
	GrooFiWorld	FriendsWorld	GrooFiWorld	FriendsWorld
1. Percentage of non-interacting dyads	2	18	0	0
2. Berger-Parker Dominance index (one top groomer)	0.19	0.26	0.17	0.16
3. Berger-Parker Dominance index (three top groomers)	0.44	0.57	0.42	0.43
4. Stability of friends (%)	37	51	28	32

Results are average of ten runs

this was not the case for low intensity of aggression (Tables 8 and 9, C).

Discussion

In FriendsWorld emerge all of the patterns of dominance style, namely of affiliation, aggression, reciprocation, and interchange of grooming and support, as well as their respective differences between high and low intensity of aggression (Tables 2 and 3). The addition of 'social bonding' and the tendency to follow 'friends' had only a quantitative effect on the patterns of reciprocation and interchange: In FriendsWorld, these patterns became significantly stronger than in GrooFiWorld but only at high intensity of aggression (Tables 4 and 5, C). Thus, the mere act of individuals moving towards their most frequent grooming partners results in a reinforcement of reciprocation and interchange of grooming and support.

In FriendsWorld, reciprocation and interchange of grooming and support become stronger than in GrooFiWorld due to the increased frequency of interactions of individuals with their top 25 % grooming partners than with other group members (Tables 8 and 9, C). Indeed, individuals in FriendsWorld, (1) are more selective in their interaction partners (2–3 in Table 6) and (2) keep the same top 25 % of grooming partners over a longer time period (4 in Table 6) than in GrooFiWorld. Thus, the tendency of individuals to move towards their most frequent grooming partners causes individuals to interact more often with those with whom they are 'socially bonded.'

However, in FriendsWorld, reciprocity and interchange are not only a consequence of individuals following their top 25 % most frequent grooming partners but also of the socio-spatial structure of the group (Puga-Gonzalez et al. 2009). Thus, in FriendsWorld, there are two different mechanisms promoting reciprocation and interchange of grooming and support. First, as in GrooFiWorld, reciprocity and interchange emerge due to the socio-spatial structure and due to proximity-based interactions like in symmetry-based reciprocity (Puga-Gonzalez et al. 2009; Hemelrijk and Puga-Gonzalez 2012). Second, due to 'social bonding,' individuals prefer to move towards their top grooming partners, and this reinforces the patterns of reciprocation and interchange of grooming and support. Hence, the GrooFiWorld model suggests how reciprocation and interchange may have emerged once primates started living in groups, i.e., through the emergent socio-spatial structure of the group. After this initial assortment of individuals in space, social bonding may further promote the differentiation of social interactions and consequently reinforce patterns of reciprocation and interchange, as shown by our present model FriendsWorld.

Table 7 Comparison of the values of diversity of partners and stability of friends

	GrooFiWorld	FriendsWorld	GrooFiWorld vs FriendsWorld	
	A. High vs. low	B. High vs. low	C. High	D. Low
1. Percentage of non-interacting dyads	U=55 NS	U=70*	U=66 NS	U=50 NS
2. Berger-Parker dominance index (one top groomer)	U=61 NS	U=89**	U=72	U=71 NS
3. Berger-Parker dominance index (three top groomer)	U=53 NS	U=83**	U=73*	U=70 NS
4. Stability of friends	U=694***	U=736.5***	U=634.5**	U=612.5*

Comparison between high and low intensities of aggression in (A) GrooFiWorld and (B) FriendsWorld, and between FriendsWorld and GrooFiWorld at (C) high and (D) low intensities of aggression. Mann–Whitney U test

NS not significant

*p<0.05, **p<0.01, ***p<0.001

Table 8 Interaction frequencies between friends and non-friends in GrooFiWorld and FriendsWorld

	High intensity of aggression				Low intensity of aggression			
	GrooFiWorld		FriendsWorld		GrooFiWorld		FriendsWorld	
	Friends	Non-friends	Friends	Non-friends	Friends	Non-friends	Friends	Non-friends
Time spent attacking (%)	62	38	73	27	63	37	63	37
Time spent supporting (%)	68	32	76	24	63	37	62	38

Results are average of ten runs

In contrast to high intensity of aggression, at low intensity reciprocation and interchange did not become stronger in FriendsWorld than in GrooFiWorld. This was probably due to the fact that at low intensity of aggression individuals in FriendsWorld interact with their top 25 % grooming partners as frequent as in GrooFiWorld (Tables 8 and 9, C). A combination of factors may account for this result. In both models, GrooFiWorld and FriendsWorld, at low intensity of aggression, there is no correlation between dominant individuals and centrality which means that the spatial structure of the group is less rigid than at high intensity of aggression (4 in Table 3). Individuals, therefore, may interact equally often with everybody. In addition, because of the shallow dominance hierarchy, individuals experience more or less the same risk when interacting with a dominant or a subordinate individual, and as a result, they may distribute their grooming more uniformly among group members. This causes individuals to switch their most preferred grooming partners frequently. Since individuals switch their top 25 % grooming partners in FriendsWorld as frequently as in GrooFiWorld, the degree of reciprocation and interchange is also similar. Thus, the FriendsWorld model predicts that, in species or groups with a tolerant dominance style, friendships will be less stable than in those with an intolerant dominance style (Tables 6 and 7).

Table 9 Comparison of interaction frequencies

	Intensity of aggression	
	High	Low
A. GrooFiWorld (friends vs. non-friends)		
Time spent attacking (%)	U=100***	U=100***
Time spent supporting (%)	U=100***	U=100***
B. FriendsWorld (friends vs. non-friends)		
Time spent attacking (%)	U=100***	U=100***
Time spent supporting (%)	U=100***	U=100***
C. GrooFiWorld vs. FriendsWorld (friends vs. friends)		
Time spent attacking (%)	U=100***	U=52 NS
Time spent supporting (%)	U=100***	U=50 NS

Comparison between friends and non-friends at high and low intensities of aggression in (A) GrooFiWorld, (B) FriendsWorld, and (C) between friends in FriendsWorld and friends in GrooFiWorld. Mann–Whitney U test

NS not significant

*p<0.05, **p<0.01, ***p<0.001

Both mechanisms, 'follow-your-friends' and emotional bookkeeping, lead to the same prediction that 'friends' will reciprocate and interchange social services. It is difficult to distinguish which mechanism (if any) may be operating in real primates. The FriendsWorld model, however, also delivers predictions which are unexpected in the framework of emotional bookkeeping and seem to contradict it. Emotional bookkeeping suggests that a positive emotional bond should elicit the exchange of positive social behaviors (Schino and Aureli 2009, 2010). In FriendsWorld, however, individuals do not only exchange beneficial acts for other beneficial acts (of the same type or a different type, such as grooming for the receipt of support), but also 'exchange' beneficial acts for harmful ones. For instance, individuals fight more with their 'friends' than with their 'non-friends' (Tables 8 and 9), and they also interchange grooming for the receipt of aggression (Table 10). Evidence for the interchange between grooming and harmful aggressive acts has recently been demonstrated. In Japanese macaques, adult females directed more grooming to those partners from whom they received aggression more often (Schino et al. 2005); in Barbary macaques, adult females were groomed more often by those whom they attacked more frequently (Carne et al. 2011); also, female bonnet macaques interchange grooming for both dyadic aggression and opposition in fights (IP-G et al. unpublished data).

We are aware of at least two theoretical studies of 'emotional bookkeeping' based on individual-based models of social behavior of primates. In one model, individuals have a partner preference based on the memory of previous socio-positive interactions which leads to differentiated relationships and consequently to cooperation (Campenni and Schino 2014). In the other model, individuals develop 'like attitudes' which are partner-specific and depend on the frequency of grooming received. The 'like attitude' regulates the individual's behavior (i.e., odds of grooming its partner or not)

Table 10 Interchange of grooming for harmful acts of aggression (dyadic aggression and opposition) in GrooFiWorld and FriendsWorld

	High intensity of aggression		Low intensity of aggression	
	GrooFiWorld	FriendsWorld	GrooFiWorld	FriendsWorld
Groom given for aggression received	0.63***	0.75***	0.53***	0.55***
	U=87***		U=50 NS	
Groom given for opposition received	0.45***	0.64***	0.34**	0.36**
	U=100***		U=69 NS	
Aggression given for groom received	0.46***	0.55***	0.53***	0.56***
	U=77**		U=70 NS	
Opposition given for groom received	0.25**	0.49**	0.38***	0.39***
	U=94***		U=57 NS	

Tau-Kr matrix correlations results are average of ten runs; p values are combined via the improved Bonferroni method. Mann–Whitney U test was used to test for differences between GrooFiWorld and FriendsWorld

NS not significant

*p<0.05, **p<0.01, ***p<0.001

and leads to reciprocal grooming relationships (Evers et al. 2014). Like in these two models, in FriendsWorld, individuals have a partner preference, i.e., they follow their friends, which are their most frequent grooming partners. In contrast to these two models, in FriendsWorld, individuals do not modify their behavior towards 'friends' and 'non-friends' in terms of repayment.

Besides reciprocating and interchanging grooming and support, in earlier studies of the GrooFiWorld model, we have shown that it generates also many other patterns of affiliation and aggression that resemble those of primates, especially macaques. For instance, in the model, individuals statistically 'reconcile' with former opponents and do so more with 'friends' than with others, 'console' victims, and 'appease' aggressors (Puga-Gonzalez et al. 2009, 2014; Hemelrijk and Puga-Gonzalez 2012). Furthermore, when in the model, intensity of aggression is set high instead of low and patterns change from those resembling a tolerant dominant style to those resembling an intolerant dominant style (Puga-Gonzalez et al. 2009). In our present study, we demonstrate further that if we also represent in the model 'social bonding' by making individuals tend to follow their most frequent grooming partners, this reinforces reciprocation and interchange of grooming and support. This mechanism, 'follow-your-friends,' leads to predictions that are unexpected in the framework of emotional bookkeeping and can be tested using existing empirical data. Thus, these predictions may help us to distinguish between the mechanism of 'follow-your-friends' and emotional bookkeeping.

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